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BULLETIN

OF THE

TORREY BOTANICAL CLUB

JANUARY, 1916

Physiological observations on *Drosera rotundifolia* *

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(WITH ELEVEN TEXT FIGURES)

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I. INTRODUCTION

The object of the work, which this paper presents, was to determine whether the bending of *Drosera* tentacles was connected with a temporary acceleration of the rate of growth or with differences of turgidity; in physiological terms, whether the bend-

* Contribution from the Osborn Botanical Laboratory.

[The BULLETIN for December (42: 651-698. *pl.* 30-33) was issued January 20, 1916.]

ing was a nutation or a variation movement. Analogy with the behavior of tendrils, which has been thoroughly investigated by Fitting, indicates that the reactions of *Drosera* are phenomena of growth, and this is substantiated by Batalin's ('77, p. 36) somewhat meager measurements. These are, in Pfeffer's words ('06, 3: 85), "not fully satisfactory." Although the primary purpose of this paper is to settle this point, a number of observations were made during the work which pertain to other matters. These minor points are of some physiological interest and will be mentioned before proceeding to the main discussion.

2. MATERIAL

The material used was collected during the months of July and August from Beaver Swamp in the city of New Haven, Connecticut. It was found advisable to use only fresh material for experimentation.

Plants of *Drosera rotundifolia* and *D. longifolia* were found growing in *Sphagnum*. In removing them, large pieces of the substratum were taken along with the plants to prevent injury to the roots and to insure their further development in the laboratory. Slight injuries to the roots cause the secretion of the glands to stop and render the tentacles inactive, so that they fail to respond to the customary stimuli. The root-hairs are particularly remarkable, for they are not restricted to a small region above the root-tip but cover the entire length of the root. They do not die, but continue to grow and function. In this way they increase the effectiveness of the small root-system.

The plants were placed in flat dishes, made wet with distilled water and covered with bell-jars. Under these conditions the development of the plants was far from normal. The rosette arrangement of the leaves was lost, a typical stem was developed by lengthening of the internodes and every trace of red pigment disappeared. No gradations from purple to green leaves were observed. All the leaves, which unfolded in the moist atmosphere and subdued light of the culture, were green. The size of the leaves diminished and their petioles made a more acute angle with the stem, causing them to point obliquely upward instead of horizontally outward.

3. PIGMENT

The red pigment of *Drosera* occurs predominantly in the leaves and the root-cap. Young leaves frequently have the pigment restricted to the glands of the tentacles. Later it appears in the epidermal cells of the marginal pedicels. Leaves of old plants often have the entire leaf-blade pigmented and, as the leaf matures, the color spreads down the petiole and often into the stalk. In general young plants are much greener than old ones, but wide variations are found.

The red pigment of *Drosera rotundifolia* and *D. longifolia* is identical with one of the pigments which Rennie ('87, '93) extracted from rhizomes of *D. Whittakeri*. Its formula is $C_{11}H_8O_5$, and it is probably trihydroxymethylnapthoquinone, since it gives the reaction of Brissemoret and Combes ('07) characteristic of α -napthoquinones.

To obtain the pigment, place a deep red leaf on a slide, add a few drops of hot alcohol, put on a cover-glass and heat directly over boiling water. The pigment is extracted from the leaf and, on the evaporation of the alcohol, it is deposited around the edges of the cover-glass. It forms crystals which are small red disks. It is insoluble in cold water, hardly soluble in cold alcohol and glacial acetic acid, but dissolves readily in boiling water, hot alcohol and ether, and to a lesser extent in benzol and carbon disulphide. It is soluble in alkalis. When a leaf is treated with ammonia, the pigment turns dark violet or brown; on standing the color fades. A timely treatment with dilute acid precipitates the pigment and restores the red color, but this does not occur after prolonged action of the ammonia. Reduction with stannous chloride and alcoholic hydrochloric acid gives a yellow product which crystallizes in needles. This is reoxidized to the original compound, when allowed to stand in alcoholic or alkaline solution exposed to the air. These properties were found for the pigment of *D. rotundifolia*. They coincide with those given by Rennie for the compound $C_{11}H_8O_5$, and confirm the suggestion of their identity put forward by Kraemer ('10, p. 285).

Experiments were made with the green plants to determine under what circumstances the pigment reappeared. Several plants of *D. longifolia* were cultivated for a month in a moist

atmosphere, without being fed with insects. They lost all traces of pigment. Six of these were fed with small flies and two days later pigment was observed in the marginal tentacles of the youngest leaves, that had just unrolled. A similar reappearance of color was observed in three other plants which caught insects. This is the opposite of the results obtained by F. Darwin ('08, p. 23) and by Büsgen ('83, p. 592), who found that plants fed with insects had much greener leaves than those which relied solely on photosynthesis for their nourishment. The contradiction may be owing to different environmental conditions, such as the chemical composition of the substrate, the intensity of the light, or the humidity of the atmosphere. The question merits further investigation.

4. HABIT

Another peculiarity observed in plants cultivated in a moist atmosphere was the peculiar habit assumed by the plant. The internodes became lengthened, and this was the case with plants exposed either to the diffuse light of the laboratory or to direct sunlight. Plants exposed to dry air were observed to retain the rosette habit under both light conditions. This shows that the rosette habit characteristic of *D. rotundifolia* is dependent upon transpiration and not upon light, as Diels ('06, p. 32) suggests. This relation represents an interesting adaptation, for as long as the plant is beneath the surface, the internodes lengthen, since transpiration is reduced to a minimum. In this way the terminal bud is brought to the surface, where rapid transpiration from the exposed leaves causes the development of a rosette.

5. PARASITES

A great many of the plants cultivated in the laboratory were destroyed by larvae accidentally brought with the material from the swamp. They were larvae of one of the cut-leaf moths or noctuids. Since the adult form has not been obtained, it has been as yet impossible to identify them. The young larvae are about a quarter of an inch long and very pale. They climb up the under side of the leaf-petioles and eat the blade from behind. In this way they avoid the tentacles which could easily catch and digest such small creatures. The larvae select the youngest

leaves and destroy the plant by eating the terminal bud. Many of the fragments of partially eaten leaves fall onto the *Sphagnum* and produce new plants by regeneration. Here again is an arrangement which may be considered a reciprocal adaptation; the larvae are protected from the leaves which could consume them, and the destruction of the plant by the larvae results in vegetative reproduction. As the larvae grow older they increase greatly in size and become green. Even after they have reached a size which renders their capture by a *Drosera* leaf impossible, they continue to crawl along the under surface and eat the leaves from behind. They become exceedingly voracious and a single insect can devour a dozen flourishing plants in two days.

6. CULTIVATION

The *Drosera* plants used for experimentation were grown in uncovered dishes exposed for at least six hours a day to direct sunlight. Small flies and other insects were placed on the leaves from time to time. The best leaves were selected for reactions and were not fed. In one remarkable instance, a house-fly was placed on a small fresh leaf which was only slightly pigmented. A copious secretion resulted which enveloped and digested the fly. After five days, however, the entire leaf-blade had disappeared, being digested by its own fluid. The plant was not vigorous and the fly was too large for the leaf, but normally anti-enzymes or other adequate means must be present to prevent autolysis.

7. MECHANICS OF MOVEMENT

(a) NORMAL DEVELOPMENT

The blade of the undeveloped *Drosera* leaf is rolled up. As it expands the marginal tentacles are seen to be bent over the blade, the glands pointing against the leaf and the pedicels arranged like rays around the edge. As the leaf grows, these tentacles increase considerably in length, the growth being greater on the adaxial side. By this means the incurved tentacles are straightened, a process which is assisted by the simultaneous flattening of the leaf-blade. When all the tentacles are straight, the leaf is mature and able to catch insects. The full grown tentacles do not increase perceptibly in length. They remain in this condition for about

two weeks, during which time their glands secrete actively. At the end of this period the tentacle begins to bend backward. In old leaves the marginal tentacles are much recurved, and in extreme cases the gland may pass through a complete revolution by the rolling up of the distal portion of the pedicel. The petiole of young leaves points up. As the leaf ages, its petiole bends down so that the mature leaf is horizontal.

The pedicels of the exterior tentacles are dorsi-ventrally flattened at the base. The abaxial side has numerous short glandular hairs distributed over its entire length. On the adaxial side they are fewer in number and are confined more or less to the base.

(b) EXPERIMENTAL METHOD

Fresh leaves which had not been previously touched were selected for experimentation. The entire plant was removed from the *Sphagnum* in which it grew and was placed in a large Stender dish. A piece of cork was fastened with sealing wax inside the dish and another piece attached to it by two pins. The petiole of the selected leaf was clamped horizontally between the two pieces of cork in such a way that the leaf-blade was vertical. The bottom of the dish was covered with water and the roots were wrapped in wet sphagnum. The cover of the Stender dish was replaced or discarded, as desired. A binocular microscope was used, because the greater distance from the objective to the object made it more convenient when the Stender dish was covered. An horizontal tentacle, which showed glandular hairs on both upper and lower sides and which was not obscured by its neighbors, was selected from the edge of the leaf opposite the petiole. Its pedicel was marked with China ink to facilitate identification.

Each tentacle was measured with a micrometer scale and drawn with a camera lucida before an experiment. The gland was then stimulated by placing upon it some object such as the leg of a fly. This was removed as soon as movement began. At each subsequent observation the time was recorded and the tentacle was sketched. This was continued at intervals until the pedicel was again straight. The tentacle was then measured for the second time with the micrometer scale.

The figures given in the tables are in hundredths of a millimeter. Measurements were made on the drawings, which were checked by the direct measurements. The time at the head of the first column shows when the gland was stimulated. The column to the right of the heavy line shows the first indication of unbending. The segments were marked off naturally by the presence of glandular hairs on the two flattened surfaces. They are numbered from the apex to the base. The segments on the concave side do not always correspond to those on the convex side.

TABLE I

	No. of Segment	10.00 A. M.	10.15 A. M.	10.35 A. M.	11.00 A. M.	11.20 A. M.	11.40 A. M.	12.00 M.	1.15 P. M.	2.00 P. M.	3.00 P. M.	3.30 P. M.	4.00 P. M.	4.30 P. M.	5.00 P. M.	7.35 P. M.	9.00 P. M.	9.10 P. M.
Abaxial side	1	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80
	2	23	23	23	23	23	25	25	25	25	25	25	25	25	25	25	25	25
	3	24	25	25	25	28	28	28	28	28	28	28	28	28	28	28	28	28
	4	29	31	31	32	34	35	35	35	35	35	35	35	35	35	34	34	34
	5	36	41	41	42	43	45	49	49	48	48	48	48	48	48	48	48	46
	6	43	51	52	53	55	57	59	59	59	59	58	57	55	55	55	55	55
	7	59	60	60	60	61	69	70	72	72	72	71	69	69	69	69	69	69
	Total . .	294	311	312	315	324	339	346	348	348	347	345	342	340	340	339	339	337
Adaxial side	1	78	78	78	78	78	78	78	78	78	78	78	78	78	78	78	78	78
	2	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	24
	3	24	25	25	25	25	25	25	25	25	25	25	25	26	26	26	27	27
	4	31	31	31	29	29	29	28	28	28	29	29	29	29	31	32	33	34
	5	40	40	40	40	40	40	40	40	41	41	41	41	41	41	43	44	46
	6	28	29	29	29	31	32	32	32	34	35	35	35	35	35	35	36	38
	7	28	28	28	28	28	28	28	28	29	31	32	33	33	34	34	35	37
	8	45	45	45	45	46	48	49	50	50	50	50	50	50	51	51	52	54
	Total . .	297	299	299	297	300	303	303	304	307	310	312	313	315	319	322	328	338

(c) EXPERIMENTAL DATA

Measurements of the dorsal and ventral sides of a tentacle in the process of bending and unbending are given in TABLE I. The tentacle was selected from next to the outermost row on a fresh, red, young leaf which was secreting copiously. The leaf had been protected during its development and was not touched, or stimulated in any other way, prior to the experiment. Its reaction is typical of the marginal tentacles on young leaves, unless perhaps it is more than usually vigorous.

The straight tentacle measured 2.94 mm. in length. The leg of a small house-fly was laid on the gland. One minute and a

half after stimulation movement was detected, whereupon the fly-leg was removed. After fifteen minutes the tentacle was well bent and the gland had moved through an angle of about fifty degrees. Marked elongation took place on the convex side near the base in Segment 6, and to a lesser extent in Segment 5. The concave side remained nearly of the same length as before. The region of bending is coincident with the region of elongation on the

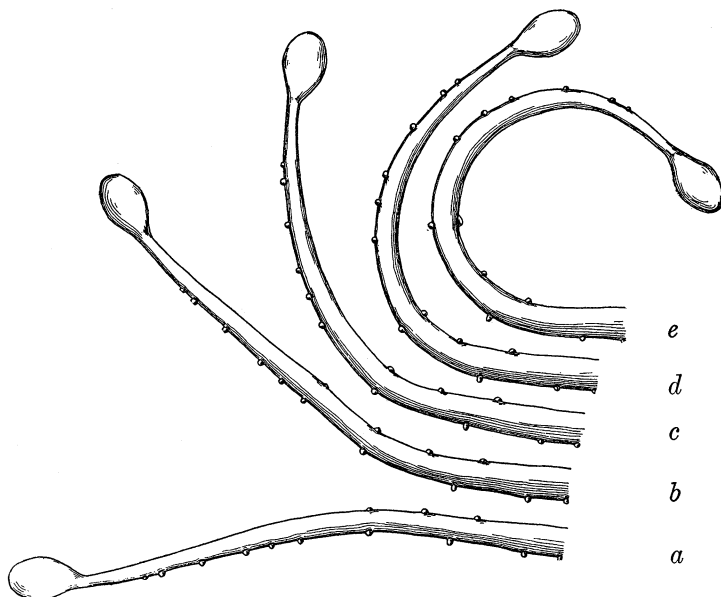


FIG. 1. Side views of a tentacle in the process of bending, $\times 22$. *a*, before stimulation; *b*, *c* and *d*, successive stages of inflexion; *e*, the fully bent tentacle.

convex side. As the tentacle continued to bend, the area of curvature and elongation was extended upward toward the gland, including Segments 4, 3, and 2, and to a lesser extent downward so as to include a portion of Segment 7. In the ultimate stage the curved region subtended an angle of approximately 215 degrees. Both sides increased in length, but the increase of the convex side was eight times that of the concave. FIG. 1 is a series of camera lucida drawings made during the inflexion of this tentacle. In *b* the bending region is seen to be restricted at first to the lower end and to extend apically in *c* and *d*. The final

condition attained 3 hours and 15 minutes after stimulation is shown in *e*.

Unbending commenced immediately. TABLE I shows that this resulted from elongation of the concave side and contraction of the convex side. The region of elongation is at first near the base in Segment 7, which lies opposite the lower portion of Segment 6 on the convex side. This region gradually extends apically. The contraction on the convex side is mostly confined to the base, and it is moreover relatively slight, being only one fourth the amount of elongation on the concave side. FIG. 2 shows the result of these alterations in length. Since the reaction commences near the base, this portion is the first to straighten;

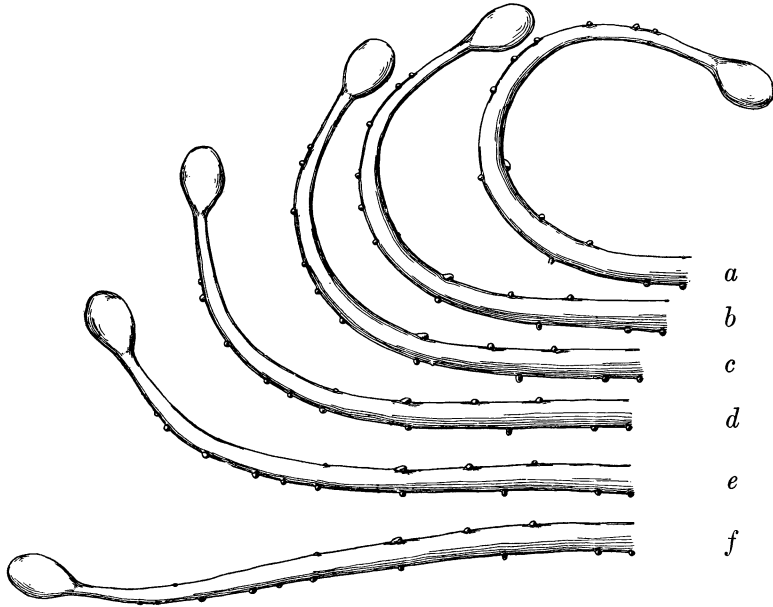


FIG. 2. Side views of the tentacle shown in FIG. 1 in the process of unbending. $\times 22$. *a-e*, successive stage in the expansion; *f*, the tentacle at the completion of the reaction.

as successive portions on the concave side further removed from the base elongate, the straight part of the pedicel lengthens. In unbending the tentacle is therefore curved in a different manner than during bending. In the latter case, the principal curve is near the base, in the former, nearer the apex. A comparison of

FIG. 1, *a* and *b*, with FIG. 2, *d* and *e*, illustrates this. The most apical part which elongated during the process of bending is the last to regain its original position. The basal portion, however, does not stop increasing its length until the entire tentacle is straight. At the end of the reaction, after 23 hours and 10 minutes, the tentacle measured 3.37 mm. It had therefore *grown* during the process of bending and unbending 0.43 mm. (See

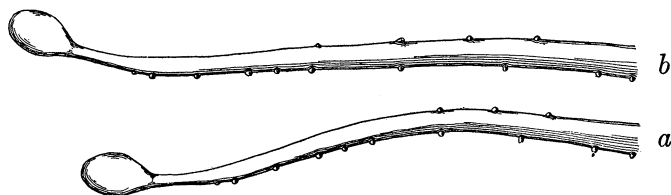


FIG. 3. Side views of the same tentacle before and after the reaction, to show the increase in length, $\times 22$. *a* is the same as FIG. 1, *a*; *b* is the same as FIG. 2, *f*.

FIG. 3). A control tentacle which had not been stimulated measured before and after the experiment 2.57 mm. Another measured 2.6 mm. They had not grown a measurable amount during the interval.

FIG. 4 is a graphical representation of the growth of the tentacle. The elongation of the abaxial side is shown by the

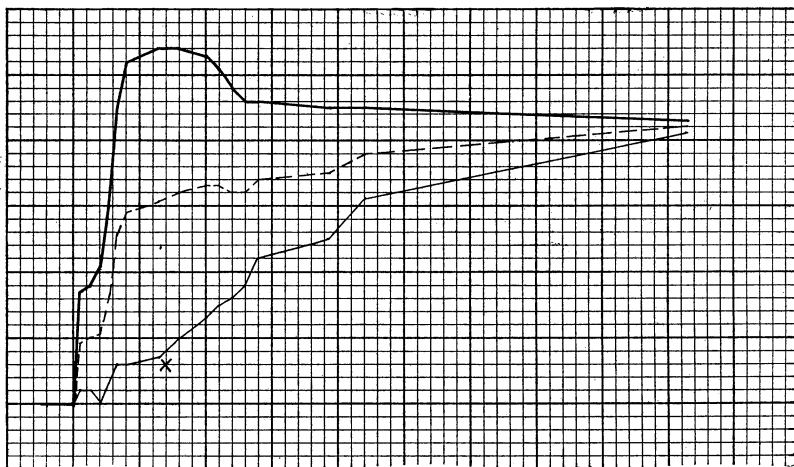


FIG. 4. A graph representing the reaction shown in FIGS. 1 and 2, drawn according to data in TABLE I. See text for explanation.

heavy line; the growth of the adaxial side is shown by the light line. The calculated growth of the median section of the tentacle is given by the broken line. The time is plotted on the abscissae; each space is thirty minutes. The changes in length are plotted on the ordinates; each space represents 0.02 mm. The reaction time is not indicated. The cross shows when the bending was completed and when unbending began. It is evident from the figure that the inflexion of the tentacle is produced by a considerable acceleration of the rate of growth on the abaxial side and in the median section. The unbending is more gradual and takes six times as long as the bending. Moreover the unbending is produced by a similar but less intense acceleration of the growth on the adaxial side and in the median section together with contraction of the abaxial side during the beginning of the process.

The reaction of another tentacle is shown in TABLE II and FIG.

TABLE II

	No. of Segment	10.16 A. M.	10.54 A. M.	11.18 A. M.	11.28 A. M.	11.31 A. M.	11.36 A. M.	12.09 P. M.	12.38 P. M.	3.58 P. M.	9.45 A. M.
Abaxial side	1	72	72	72	72	72	72	72	72	72	72
	2	118	118	118	118	118	118	119	119	119	119
	3	26	27	28	28	31	32	33	34	36	34
	4	54	54	54	58	58	58	58	59	59	58
	Total	270	271	272	276	279	280	282	284	286	283
Adaxial side	1	72	72	72	72	72	72	72	72	72	72
	2	121	121	121	121	121	121	120	120	120	121
	3	35	35	35	35	35	35	35	34	33	43
	4	38	37	37	37	36	35	35	34	34	42
	Total	266	265	265	265	264	263	262	260	259	278

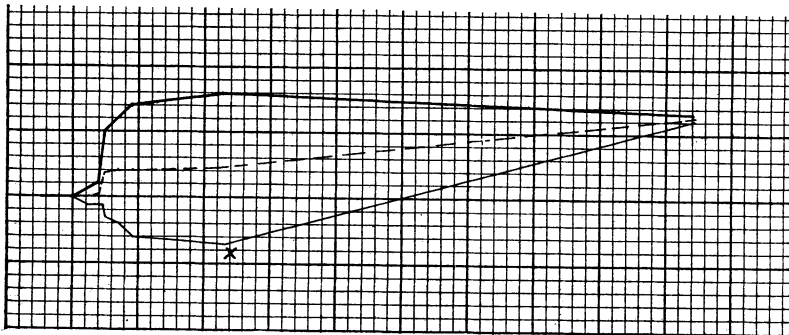


FIG. 5. A graph representing the bending and unbending of a tentacle, drawn according to data in TABLE II, and on the same scale as FIG. 4.

5. Before the experiment it measured 2.7 mm. The reaction is in all essential respects similar to the previous example, but there are important differences. The tentacle was on a mature leaf. It had not, however, been stimulated before the experiment. Bending was produced by an elongation of the convex side and the median section, accompanied by contraction of the concave side. The increase in length on the abaxial side was twice as great as the contraction of the adaxial side. The ultimate stage of bending was reached 5 hours and 45 minutes after stimulation. Unbending was caused by gradual growth on the concave side and in the median section together with slight contraction of the convex side. The original position was reached after 23 hours and 30 minutes. The tentacle then measured 2.83 mm. It had grown 0.13 mm. during the experiment.

A third example is given in TABLE III. This tentacle was in

TABLE III

	No. of Segment	3.45 P. M.	3.52 P. M.	3.55 P. M.	3.58 P. M.	4.01 P. M.	4.05 P. M.	9.20 A. M.	4.00 P. M.	9.00 A. M.
Abaxial side	1	84	84	84	84	84	84	84	84	84
	2	57	57	58	58	58	58	58	58	58
	3	37	37	37	37	40	41	42	43	43
	4	31	31	31	34	40	43	43	43	43
	5	45	47	52	53	57	57	54	50	49
	Total . . .	254	256	263	266	279	283	281	278	277
Adaxial side	1	82	82	82	82	82	82	82	82	82
	2	57	57	57	57	57	57	58	59	61
	3	58	58	58	58	59	59	60	62	66
	4	46	46	42	37	37	40	42	42	42
	5	12	12	12	12	12	12	23	23	24
	Total . . .	255	255	251	246	247	250	265	268	275

the third row from the outside, on a leaf in excellent condition. It reacted with great rapidity. Movement was detected within a minute after stimulation, and the bending was completed in twenty minutes. The table shows clearly that elongation commenced in Segment 5, the most basal portion of the abaxial side; after ten minutes Segment 4 likewise increased in length; and after three minutes more Segment 3 began to grow. The drawings in FIG. 6 show the bending, and illustrate the apical progress of the reaction. As in the previous case, the bending was produced

by acceleration of the growth on the convex side and in the median section, with contraction of the concave side.

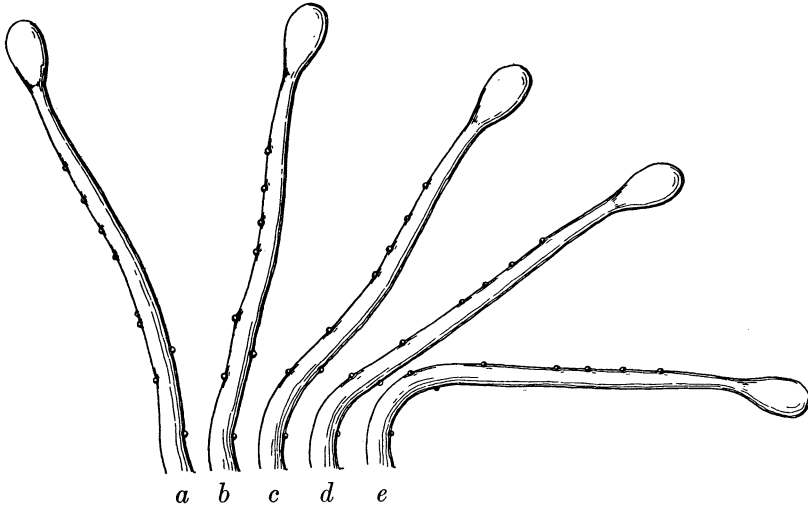


FIG. 6. Side views of a tentacle in the process of bending, $\times 22$. *a*, the straight tentacle before stimulation; *e*, the inflected tentacle twenty minutes after stimulation.

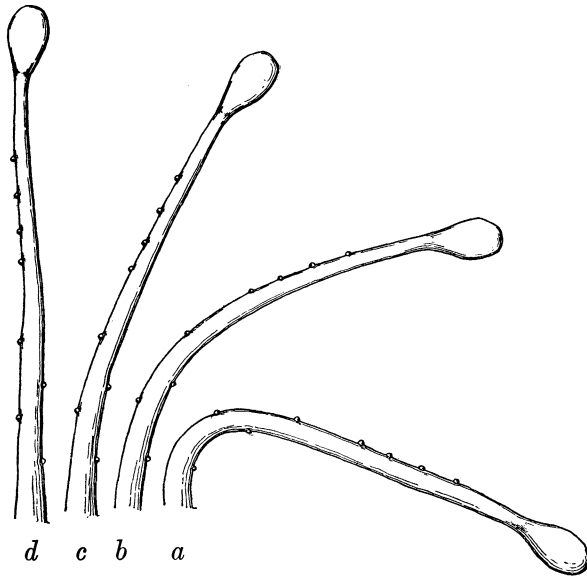


FIG. 7. Side views of the tentacle shown in FIG. 6 in the process of unbending, $\times 22$. *a*, the fully inflected tentacle; *d*, the straight tentacle at the end of the reaction.

The unbending presents no new features. FIG. 7 shows successive stages in the process and comparison with FIG. 6 emphasizes the different configuration of the bending and unbending tentacle. The tentacle grew from 2.54 mm. to 2.77 mm., an increase of 0.23 mm.

The reaction is plotted in FIG. 8. The complete reaction took 39 hours and 15 minutes, an unusually long time. This experiment is perhaps more representative than the first in that growth was confined to the lower half of the pedicel.

After a day's rest, the tentacle used in the first experiment was stimulated a second time. The leaf was still fresh and actively secreting. At the beginning of this experiment the tentacle measured 3.37 mm. The results of the reaction are shown in TABLE IV, and are represented in graphical form in FIG. 9. Movement began within two minutes. The bending was produced by elongation of the abaxial side beginning in Segment 6 and extending apically to Segments 5 and 4, and basally to a part of Segment 7. The region of elongation and curvature was shorter than in the first reaction, where it included Segments 3 and 2. The acceleration of the rate of growth was also less than during the first inflexion. The time required for the bending was increased to four hours. The time taken to regain the original position was

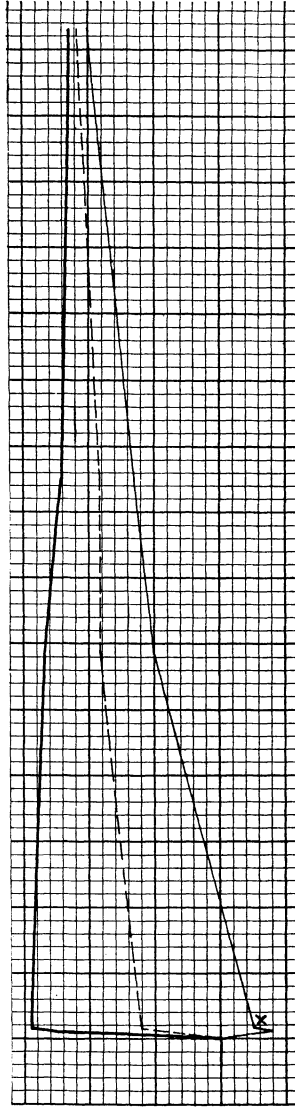


FIG. 8. A graph representing the reaction shown in Figs. 6 and 7, drawn according to data in TABLE III, on the same scale as FIG. 4.

approximately the same as before, 22 hours and 45 minutes. At the end of the reaction the tentacle measured 3.74 mm. It had increased 0.37 mm. in length. A control, that like this tentacle

TABLE IV

	No. of Segment	10.15 A. M.	10.30 A. M.	10.45 A. M.	11.00 A. M.	*11.30 A. M.	11.45 A. M.	12.45 A. M.	2.15 P. M.	3.00 P. M.	7.00 P. M.	10.10 P. M.	9.00 A. M.
Abaxial side	1	80	80	80	80	80	80	80	80	80	80	80	80
	2	25	25	25	25	25	25	25	25	25	25	25	25
	3	28	28	28	28	28	28	28	28	28	28	28	28
	4	34	35	35	35	35	36	36	36	36	36	36	36
	5	46	46	49	53	54	55	55	57	57	57	54	53
	6	55	64	64	69	69	69	69	71	71	71	71	70
	7	69	69	69	71	73	76	76	82	82	82	82	82
	Total	337	347	350	361	364	369	369	379	379	379	376	374
Adaxial side	1	78	78	78	78	78	78	78	78	78	78	79	79
	2	24	24	24	24	24	24	24	24	24	24	25	25
	3	27	27	27	27	28	28	28	28	28	28	28	28
	4	34	35	35	35	35	35	35	35	35	35	35	36
	5	46	46	47	47	47	47	47	47	47	47	53	54
	6	55	59	59	59	59	59	59	59	59	59	60	69
	7	75	75	75	75	75	76	77	78	79	84	84	84
	Total	339	344	345	345	346	347	348	349	350	355	364	375

* Controls well bent.

had made one previous inflexion, measured 2.85 mm. before and after the experiment. Another that had never reacted measured similarly 2.3 mm.

This tentacle was allowed to rest over another day and it was stimulated for the third time. At this time it measured 3.74 mm.

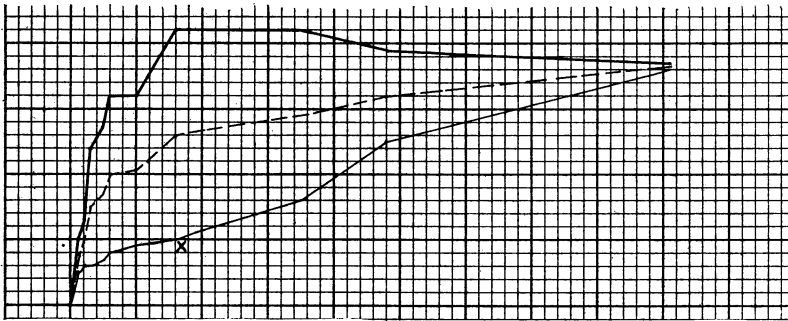


FIG. 9. A graph representing the second reaction of the tentacle shown in FIGS. 1-4; drawn according to data in TABLE IV, and on the same scale as FIG. 4.

The reaction is represented in TABLE V and FIG. 10. No movement was observed for an hour after stimulation. The region of elongation and curvature was shorter than in the second reaction.

TABLE V

	No. of Segment	12.00 M.	2.55 P. M.	7.30 P. M.	10.40 P. M.	9.15 A. M.	1.00 P. M.
Abaxial side	1	80	80	80	80	80	80
	2	89	90	92	92	92	92
	3	53	54	54	54	54	54
	4	70	79	79	79	78	77
	5	82	98	98	98	96	95
	Total	374	401	403	403	400	398
Adaxial side	1	79	79	79	79	79	79
	2	89	94	93	93	93	93
	3	54	53	54	54	54	54
	4	69	68	68	68	75	77
	5	84	84	85	85	90	93
	Total	375	378	379	379	391	396

The acceleration of growth on the convex side was less than in the previous reaction, and the tentacle was not fully bent for 7 hours and 30 minutes. It remained in this condition 2 hours and 30 minutes before unbending again. The tentacle was again straight 25 hours after stimulation. It measured 3.98 mm., an increase of 0.24 mm. After this experiment the tentacle stopped secreting, and no further reaction could be obtained.

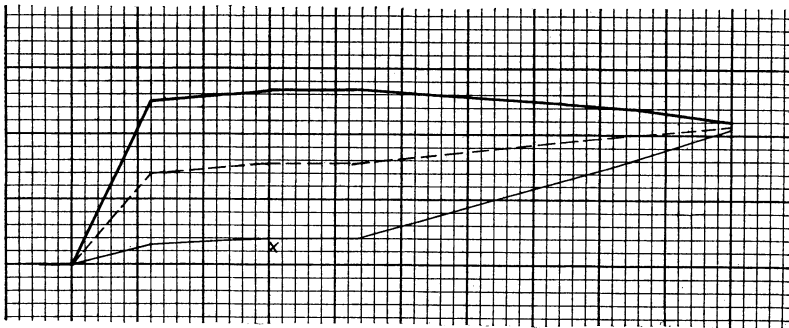


FIG. 10. A graph representing the third reaction of the same tentacle shown in FIG. 9; drawn according to data in TABLE V, and on the same scale as FIG. 4.

The results of the three successive reactions of this tentacle are summarized in TABLE VI. The increase in length for the three reactions was 0.43 mm., 0.37 mm. and 0.24 mm. The region of most intense growth moved basally. In the first reaction

TABLE VI

No. of Segment	Original Length	Length after First Bending	Amt. of Growth	Relative Amt. per Mm.	Length after Second Bending	Amt. of Growth	Relative Amt.	Length after Third Bending	Amt. of Growth	Relative Amt.
1	80	80	0	0	80	0	0	80	0	0
2	47	53	6	13	53	0	0	53	0	0
3	29	34	5	17	36	2	6	39	3	8
4	36	46	10	27	53	7	15	54	1	2
5	43	55	12	28	70	15	27	77	7	10
6	59	69	10	17	82	13	19	95	13	16
Total ...	294	337	43	15	374	37	11	398	24	6

it was in Segments 4 and 5; in the second in Segment 5; and in the third in Segment 6. The ultimate stages of bending in the three reactions are shown in FIG. 11. In each subsequent inflexion

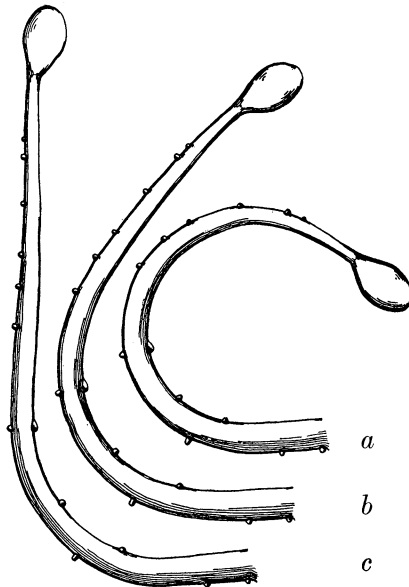


FIG. 11. The ultimate stages in three successive inflexions of the same tentacle, $\times 22$. *a*, at the end of the first inflexion; *b*, at the end of the second inflexion; *c*, at the end of the third inflexion.

the amount of bending decreased, the gland was moved through successively smaller angles and the zone of bending was restricted to shorter and more basal portions of the tentacle.

TABLE VII

No. of Segment	Original Length	Length after First Reaction	Amt. of Growth	Relative Amt. per Mm.	Length after Second Reaction	Amt. of Growth	Relative Amt.	Length after Third Reaction	Amt. of Growth	Relative Amt.
1	23	23	0	0	23	0	0	23	0	0
2	40	40	0	0	40	0	0	40	0	0
3	11	11	0	0	11	0	0	11	0	0
4	22	23	1	5	23	0	0	23	0	0
5	35	34	3	9	41	3	8	41	0	0
6	20	23	3	15	25	2	8	27	2	8
7	21	34	13	62	41	7	21	59	18	44
Total ...	172	192	20	17	204	12	6	224	20	10

TABLE VII shows the growth of another tentacle during three successive reactions. The respective elongations were 0.2 mm., 0.12 mm. and 0.2 mm. During the first reaction Segments 4 to 7 grew. The rate of growth was most intense in the lowest segment and decreased toward the apex. The second reaction was produced by growth in Segments 5 to 7. Segment 4 did not elongate. Here again the most intense growth was at the base. In the third reaction growth was confined to Segments 6 and 7, and was considerably more intense in the latter. Segments 4 and 5 did not increase in length. The tentacle was again stimulated but did not bend.

TABLE VIII

No. of Segment	Original Length	Length After First Reaction	Amt. of Growth	Relative Amt. per Mm.	Length After Second Reaction	Amt. of Growth	Relative Amt.	Length After Third Reaction	Amt. of Growth	Relative Amt.
1	85	85	0	0	85	0	0	85	0	0
2	52	54	2	4	54	0	0	54	0	0
3	82	88	6	7	89	1	1	89	0	0
4	23	25	2	9	33	8	32	38	5	15
5	36	42	6	17	51	9	21	60	9	18
Total ...	278	294	16	6	312	18	6	326	14	15

A third example of this sort is given in TABLE VIII. The reaction time of the first inflexion was 1 minute, 40 seconds. Segments 2 to 5 increased in length. The rate of growth was

greatest in the lowest segment and decreased apically. The second reaction was produced the day following the first. The reaction time was 1 minute, 30 seconds. Growth occurred in Segments 3 to 5. Segment 2 had stopped growing. The third reaction took place two days after the first one. More than an hour elapsed before movement was detected. Growth was confined to Segments 4 and 5. No elongation of Segments 2 and 3 took place. The third unbending of the tentacle was exceedingly slow, and the pedicel did not regain its original position until three days after stimulation. A fourth reaction could not be induced. The elongations accompanying the first, second and third inflexions were nearly constant, being 0.16 mm., 0.18 mm. and 0.14 mm., respectively.

TABLE IX

No. of Segment	Original Length	Length after First Reaction	Amt. of Growth	Relative Amt.	Length after Second Reaction	Amt. of Growth	Relative Amt.
1	80	80	0	0	80	0	0
2	19	20	1	5	20	0	0
3	20	21	1	5	21	0	0
4	16	18	2	13	18	0	0
5	37	43	6	16	44	1	2
6	32	41	9	28	43	2	5
7	34	44	10	29	49	5	11
Total . . .	238	267	29	12	275	8	3

TABLE IX gives the growth during two successive reactions of a tentacle. The growing region is much more restricted in the second than in the first bending. In both cases the rate of growth increases toward the base of the pedicel.

(d) DISCUSSION

i. *Bending*

The bending of a *Drosera* tentacle is produced by an acceleration of the rate of growth, which extends from the convex side through the middle of the tentacle. In some cases the concave side is likewise included, so that the entire cross-section of the pedicel participates. In other cases the region of accelerated growth stops at a so-called neutral line, somewhere between the middle and the concave side. Under such circumstances the con-

cave side becomes shorter, probably as a result of compression. The acceleration is greatest on the convex surface and diminishes toward the concave. This difference in the rate of growth produces the bending when the acceleration extends all the way through the pedicel and includes the concave surface. If a neutral line is present, it presumably serves as a brace against which the elongation of the convex side acts.

The increase in the rate of growth begins in a part of the pedicel at or near its base, whence it moves toward the gland, widening its scope until one to two thirds of the pedicel is involved. The gland and the adjacent portion of the pedicel do not grow. C. Darwin ('08, p. 9) states that the distal half remains straight in all cases; but growth is not always as confined as he indicates, for in one case (TABLE VIII) 70 per cent of the tentacle grew, and in another (TABLE I) 73 per cent. If the place where the reaction begins is not the most basal portion of the pedicel, the acceleration of the rate of growth extends also a short distance in the direction of the leaf-blade (TABLE I). Those regions where the reaction commences have the highest rate of growth and are involved in the reaction for the greatest length of time: consequently they grow most, so that the amount of elongation is greatest at the base and decreases toward the apex. Ordinarily, bending is confined to one place, but in some of the long marginal tentacles the pedicel curves in two places—in the middle and again at the base (cf. C. Darwin, '08, p. 206). This is particularly characteristic of those tentacles which have the gland imbedded on the upper side of the pedicel, instead of at the apex.

The amount of bending is determined by two factors; the difference between the lengths of the convex and concave sides, and the thickness of the bending region. An increase in the former augments, in the latter diminishes the amount of bending. The longest tentacles bend most, since their growing region has the largest dimensions. The gland may be moved through a wide angle, for example 215 degrees as shown in FIG. 2. C. Darwin ('08, p. 9) describes an instance of movement through an angle of 270 degrees. The time required for bending is very variable. It may be nearly six hours (TABLE II, FIG. 5), or only twenty minutes (TABLE III, FIGS. 6, 7 and 8). C. Darwin ('08, p. 23) once saw inflexion finished in 17 minutes, 30 seconds.

In all cases of direct stimulation of the gland, the bending of *Drosera* tentacles is nastic; the inflected gland always points toward the center of the leaf. The stimulus may be contact, heat, injury or some chemical substance in solution.

When a tentacle reacts to a single stimulation, it begins to unbend immediately after the ultimate degree of inflexion has been reached. This is the case when the gland has been irritated by contact with some object for a limited space of time. If the source of stimulation is not removed, as for example when an insect is caught and digested, the tentacle remains inflected for a period varying from one to eleven days, according to C. Darwin ('08, pp. 11, 195). During the interval between bending and unbending the tentacle does not grow in length.

ii. *Unbending*

The unbending of the tentacle is accompanied by an increase in the rate of growth on the concave side and in the median section. The convex side always contracts so that the so-called neutral line exists somewhere between it and the middle of the tentacle. The acceleration of the rate of growth is characterized by a transverse distribution which is exactly opposite that accompanying bending. Its longitudinal distribution is however identical. The increase in the rate of growth commences opposite that basal portion of the convex side which reacted first, and extends as far apically. Growth is most rapid near the base and becomes less intense toward the gland. The contraction of the convex side is usually restricted to a short basal region.

It frequently happens that the concave grows less than the convex side, since the latter is compressed during the expansion of the tentacle. The concave side may undergo a certain amount of compression during the inflexion of the tentacle, so that the two sides grow and contract approximately equal amounts. The unbending proceeds much more slowly than the bending.

In all probability the unbending of *Drosera* tentacles is autotropic (cf. Fitting, '03, p. 612). The stimulus perceived is the inequality of conditions, pressure, tissue-tension, etc., which is produced on the opposite sides of the originally straight tentacle by its bending. The unbending is therefore of a tropic nature,

since it is a reaction in response to differences existing on the opposite sides of the tentacle. The inflexion and expansion of a *Drosera* tentacle present a remarkable instance of a practically continuous reaction, produced by a single mechanism, but caused by two stimuli of different nature, so that it is partly nastic and partly tropic.

iii. *Growth and Turgidity*

Since the movement of a *Drosera* tentacle is the result of growth, it is always longer at the end of a reaction than at the beginning. The amount of elongation varies from 0.1 mm. to 0.5 mm. This suggests a simple demonstration to show that the reaction is accompanied by growth. If a single tentacle on a leaf is stimulated, it will project a noticeable distance beyond its fellows after regaining its original position. In the field, a *Drosera* leaf frequently has some tentacles longer than other ones in the same row. These inequalities are the result of growth attendant upon reaction, for all the tentacles in one row remain of equal length if not stimulated. Sometimes a small insect is caught by a single exterior tentacle, which carries it to the center of the leaf. The insect is, however, too minute to cause a sufficient impulse to be conducted from the discal to the other marginal tentacles. They do not bend, so that after the reaction is completed they are not as long as the tentacle which was inflected.

Turgidity does not play a part in the movement of the tentacles. This was proved by plasmolyzing bent tentacles in 20 per cent salt solution. The plasmolyzed tentacles remained bent.

A comparison of FIGS. 4, 5 and 8 with graphs of Fitting, which show the haptotropic reactions of tendrils of *Sicyos angulatus* (Fitting, '02, p. 378), of *Passiflora gracilis* (Fitting, '03, p. 577, fig. 6) and of *Pilogyne suavis* (*ibid.*, p. 578, fig. 7), shows that the mechanics of movement in tendrils and tentacles are the same. Similar figures are shown by Wiedersheim for photonastic reactions of leaves of *Impatiens parviflora* (Wiedersheim, '04, p. 241, fig. 1; p. 242, fig. 2; p. 244, fig. 5), and for thermonastic reactions of the perianth leaves of the tulip (*ibid.*, p. 250, fig. 8) and the crocus (*ibid.*, p. 254, fig. 10; p. 255, fig. 12). It is clear that all these reactions are produced by the same mechanism; rapid growth on the convex side and in the median section with attendant contrac-

tion or a slower rate of growth (*ibid.*, p. 255, *fig. 12*) on the concave side. *Drosera* tentacles are characterized by a contraction of the convex side during expansion; this occurred in one case of a leaf of *Impatiens parviflora* (*ibid.*, p. 242, *fig. 2*).

iv. *Conductivity*

The reaction time represents the interval necessary for the latent period and the conduction of an impulse from the gland to the region where the reaction commences. This region has been shown to be a basal portion of the pedicel, so that the impulse is conducted the entire length of the tentacle. The reaction time usually varies from one to two minutes. C. Darwin ('08, pp. 10, 191) saw movement ten seconds after stimulation. This shows that the rate of conduction can be quite high, for assuming the length of the tentacle (which Darwin does not give) to be 2 mm., the rate of conduction would be 0.2 mm. per second, which is faster than any instance given for the haptotropic reaction of tendrils (Fitting, '04, p. 424). The rate of conduction in tentacles is generally much less (cf. Pfeffer, '06, Vol. III, pp. 93, 94). It should be emphasized that in *Drosera* tentacles stimuli are perceived by cells which are fully grown, and which undergo no further development.

It has not been definitely settled through what tissue impulses are conducted in *Drosera*, but in any case an impulse, in being conducted from the gland to the base of a tentacle, must pass through cells which later react, without producing a response in them. These cells apparently respond only to a secondary impulse released in the basal cells by the impulse conducted directly from the gland. This secondary impulse is conducted in the reverse direction, from the base toward the apex.

v. *Second and Third Reactions*

A tentacle is capable of reacting several times in succession. C. Darwin ('08, pp. 11, 19) observed a leaf inflected three times over insects, and suggested the possibility of more reactions. It is probable, however, that a leaf can clasp insects a greater number of times than any individual tentacle can react, because the capture of such prey does not always necessitate the cooperation

of all the tentacles. Those which remain inactive at one time, might bend on a subsequent occasion. However this may be, no tentacle has been observed to react the fourth time.

The second and third reactions of a tentacle are essentially similar to the first. After two reactions a tentacle is much less sensitive than before, as is shown by the increased reaction time. Each subsequent bending takes longer (cf. C. Darwin, '08, p. 19), but the original position is regained in approximately the same time. The amount of growth does not vary according to any definite rule. It depends rather on external conditions and is apparently uninfluenced by the age of the tentacle. If the external conditions are constant, the amount of growth remains the same. In one example (TABLE VIII) this was approximately the case, the increase in length for the first, second and third reactions being 0.16 mm., 0.18 mm. and 0.14 mm. respectively.

The region of growth is however more restricted in each subsequent reaction, and is confined to more basal portions of the tentacle. TABLE VII shows that 57 per cent of the tentacle grew in length during the first inflexion, 50 per cent during the second, and 32 per cent during the third. In another instance (TABLE VIII) the regions of growth were successively 70, 53, and 27 per cent of the length of the tentacle. In each reaction a certain portion of the tentacle becomes fully grown. A *Drosera* tentacle is therefore characterized by intercalary, basipetal growth. Because of this, the number of inflexions which a tentacle can make must necessarily be limited. It is therefore highly probable that a tentacle would bend a fourth time only under very exceptional circumstances.

Since growth is limited to more basal regions, the thickness of the reacting portion is greater at each successive inflexion. Moreover the greatest difference between the lengths of the opposite sides tends to decrease. Both of these factors cooperate in reducing the amount of bending, so that the gland is moved through successively smaller angles, as shown in Fig. 11.

vi. *Nastic reactions*

In all the experiments described, the glands of the marginal tentacles were stimulated directly, but reactions follow likewise

in response to impulses received by the discal tentacles and conducted to the marginal ones. The mechanism by which these reactions are carried out is identical with that described above.

Numerous experiments were made to determine if the marginal tentacles bent toward the source of stimulation. The discal tentacles on one side of a leaf were stimulated and most of the marginal tentacles which reacted to the conducted impulse, in bending toward the center of the leaf bent likewise in the direction of the source of excitement. In a number of such cases, however, marginal tentacles were observed to bend toward the center of the leaf in a direction different from the point of excitement. One or two instances in which the tentacles bent slightly in the direction of the source of excitement and not toward the center of the leaf seemed to be purely accidental and due rather to irregularities in the contour of the leaf. Nitschke ('60, p. 240) and C. Darwin ('08, p. 198 and *fig. 10*) noticed that when a gland on one side of the disk was stimulated, "the surrounding tentacles" bent to the point of excitement and not to the center of the leaf. The statement by Darwin together with his figure has generally been understood to include the marginal tentacles. He says, however ('08, p. 200): "It is, perhaps, owing to the exterior pedicels being much flattened that they do not bend quite so accurately to the point of excitement as the more central ones." I am convinced that the peripheral tentacles seldom if ever carry out tropic movements.

vii. *Discal Tentacles*

The discal tentacles differ both anatomically and physiologically from the marginal tentacles. The latter are dorsi-ventral and nastic, the former are radial and tropic. The central tentacles do not bend in response to a direct stimulus, but only to a conducted impulse, and always toward the point of excitement. The method used for investigating the mechanics of the movement of the marginal tentacles is not adapted for studying them in the central tentacles. In all probability, however, their movements are likewise the result of differential growth on opposite sides. The angle of curvature is in any case slight. This and the small diameter of the tentacles indicate that the amount of growth is

small. The bending region is confined to a very short basal portion of the pedicel.

Transitions from exterior to central tentacles occur, which exhibit intermediate conditions not only in their structure but also in their behavior. It is probable that some of these tentacles are both nastic and tropic.

8. SUMMARY

1. The red pigment which is found in the leaves and roots of *Drosera rotundifolia* is probably trihydroxymethylnapthoquinone.

2. The rosette habit is conditioned by transpiration.

3. The inflexion of *Drosera* tentacles is produced by an acceleration of the rate of growth on the convex side and in the median section. The unbending is caused by an increase in the rate of growth on the concave side and in the median section, accompanied by compression of the convex side.

4. In both cases the acceleration commences near the base and extends toward the gland. The amount of growth is greatest near the base and decreases apically.

5. A tentacle is capable of reacting three times. During each reaction an apical portion of the bending region becomes fully grown. *Drosera* tentacles have intercalary, basipetal growth.

6. The bending of the exterior tentacles is nastic; of the central tentacles, tropic. The unbending is in all cases owing to autotropism.

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LITERATURE CITED

- Batalin, A.** ('77). Mechanik der Bewegungen der insektenfressenden Pflanzen. *Flora* **60**: 33-39; 54-58; 65-73; 105-111; 129-154.
- Brissemoret, A., & Combes, R.** ('07). Sur une réaction des oxyquinones. *Jour. Pharm. et Chim.* VI. **25**: 53-58.
- Büsgen, M.** ('83). Die Bedeutung des Insektenfanges für *Drosera rotundifolia*. *Bot. Zeit.* **41**: 569-577; 585-594.
- Darwin, C.** ('08). *Insectivorous plants*. Revised by F. Darwin. London.
- Darwin, F.** ('08). Experiments on the nutrition of *Drosera rotundifolia*. *Jour. Linn. Soc. Bot.* **17**: 17-32.

- Diels, L.** ('06). Droseraceae. Engler's Pflanzenreich 4¹¹². Leipzig.
- Fitting, H.** ('02). Untersuchungen über den Haptotropismus der Ranken. Ber. d. Bot. Ges. 20: 373-382.
- Fitting, H.** ('03). Untersuchungen über den Haptotropismus der Ranken. Jahrb. Wiss. Bot. 38: 545-634.
- Fitting, H.** ('04). Weitere Untersuchungen zur Physiologie der Ranken. Jahrb. Wiss. Bot. 39: 424-526.
- Kraemer, H.** ('10). A text-book of botany and pharmacognosy. Fourth edition. Philadelphia.
- Nitschke, T.** ('60). Ueber die Reizbarkeit der Blätter von *Drosera rotundifolia*. Bot. Zeit. 18: 229-234; 237-243; 245-250.
- Pfeffer, W.** ('06). The physiology of plants. English translation. Oxford.
- Rennie, E. D.** ('87). The coloring matter of *Drosera Whittakeri*. Jour. Chem. Soc. 51: 371-377.
- Rennie, E. D.** ('93). The coloring matters of *Drosera Whittakeri*. Jour. Chem. Soc. 63: 1083-1089.
- Wiedersheim, W.** ('04). Studien über photonastische und thermonastische Bewegungen. Jahrb. Wiss. Bot. 40: 230-274.